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Understanding macroinvertebrate metacommunity organization using a nested study design across a mountainous river network

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ABSTRACT

Metacommunity ecology highlights the importance of integrating simultaneously environmental filtering and spatial processes, such as mass effects and dispersal limitation, into investigation of community assembly. However, few studies to date have tried to examine mass effects and dispersal limitation as independent ecological mechanisms along with environmental filtering in shaping biological communities in river networks. We examined the relative importance of three factor groups, i.e., environmental variables, within-river spatial factors (indicative of mass effects) and basin identity (referring to dispersal limitation) on a macroinvertebrate metacommunity and nine trait-based deconstructed sub-metacommunities from seven subtropical rivers. We applied redundancy analysis and variance partitioning to reveal the pure and shared effects of the three groups of factors on community variation. Environmental filtering, mass effects and dispersal limitation were all significant mechanisms affecting variation in macroinvertebrate communities, but their relative importance depended on biological traits. Environmental filtering explained more of the variation in the whole metacommunity, tolerant taxa and macroinvertebrate groups with weak dispersal ability (i.e., aquatic dispersal, aerial passive dispersal and large body size). In contrast, mass effects accounted for more variation in the communities of intolerant taxa and macroinvertebrate groups with strong dispersal ability (i.e., aerial active dispersal mode and medium body size). Dispersal limitation was more influential for sub-communities of moderately tolerant taxa and large-sized taxa. Our study highlights that simultaneously accounting for different spatial processes and using a trait-based approach are essential to improve our understanding of community assembly in river networks.

1. Introduction

Quantifying the ecological processes regulating community assembly has been a central issue in community ecology for a long time (Chase, 2003). In the past few decades, focus has been on niche-based processes, whereby biotic (e.g., competition, predation and mutualism) and abiotic (e.g., environmental factors) factors at local scales are of prime importance in structuring biological communities (Chesson, 2000). Recently, it has been observed that dispersal-related processes at regional scale also strongly influence community structure (Mcgill et al., 2006). These two sets of processes, however, are not mutually exclusive and should be integrated into community assembly research (Vergnonet al., 2009; Logue et al., 2011; Leibold et al., 2017). In this scenario, the metacommunity theory highlights the importance of considering ecological events at multiple nested scales, providing a framework combining niche-based (e.g., environmental filtering) and spatial processes (e.g., dispersal limitation and mass effects) into the exploration of community assembly (Leibold et al., 2004; Cottenie, 2005).

Different ecological processes usually regulate community structure in combination, but their relative importance may largely depend on the spatial extent of the study area (Rocha et al., 2017; Tornero et al., 2018). Theoretically and empirically, the influence of environmental filtering on community structure could be expected to peak at intermediate spatial extents (e.g., 10^2 to 10^5 km^2), where dispersal rates are neither too high nor too low, and most individuals can reach optimal habitat patches (Leibold et al., 2004; Heino, 2011). Mass effects usually become influential at small spatial extents (e.g., 1 to 10^2 km^2), where suboptimal

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patches support some individuals of a species irrespective of their suitability owing to continuous flux of individuals dispersing from nearby optimal habitat patches (Mouquet and Loreau, 2003; Heino et al., 2015). On the contrary, dispersal limitation should increase in its importance at relatively large spatial extents (e.g., 10^5 km^2 to continent), where between-site distance, geographical barriers or limited dispersal capacity prevent species to track variation in local environmental conditions (Shurin et al., 2009; Garcia-Giron et al., 2019).

One commonly used approach in metacommunity research has been testing the relative contribution of environmental filtering and spatial processes by using multivariate constrained ordination and associated variation partitioning procedures (Smith and Lundholm, 2010; Legendre et al., 2012). However, it is generally difficult to distinguish spatial structuring resulting from mass effects or dispersal limitation, because both processes can generate spatial signals in metacommunity patterns and may interfere with the signal of environmental filtering (Heino et al., 2017a; Sarremejane et al., 2017). Fortunately, this issue can be partly resolved by focusing on a nested study design comprising multiple spatial scales, where dispersal-related processes may be assigned into those potentially active at within-region and among-regions scales (Declerck et al., 2011; Heino et al., 2017b). Since each ecological process may occur at optimal spatial extent (the issue of scale dependency mentioned above), one may expect that mass effects should prevail at the fine within-region scale, while dispersal limitation would exert stronger control over metacommunity structure at the large among-regions scale with largely insurmountable physical barriers for dispersing organisms (Chaparro et al., 2018; Li et al., 2020).

Community assembly research also benefits from decomposing a metacommunity dataset into several relatively homogenous groups (i.e., sub-metacommunities) based on biological traits (i.e., the deconstructive approach) (Grönroos et al., 2013). Fundamentally, the coexistence and maintenance of a species in local communities depend on their biological traits (Lindholm et al., 2018). For instance, dispersal-related traits determine if a species can reach a certain locality, thus affecting species distribution and diversity patterns (Cañedo-Argüelles et al., 2015; Kärnä et al., 2015; Li et al., 2018). Meanwhile, traits related to environmental tolerance determine if a species can survive in an environment once it has arrived there (Whittier and Sickle, 2010; Chang et al., 2014). Therefore, it can be conjectured that biological groups with distinct traits would show different sensitivity to challenges posed by geographical distance and environmental gradients, thus being controlled by different assembly mechanisms. Recently, a growing number of studies have focused on community assembly using this trait-based deconstructive approach (Alahuhta et al., 2014; Tolonen et al., 2016; De Campos et al., 2018; Lindholm et al., 2018). For example, some previous studies that focused on dispersal traits found that environmental filtering played more important roles for strong/active dispersers than for weak/passive dispersers, while the opposite was shown to be true for spatial processes (Heino, 2013; Csercsa et al., 2019). Likewise, other biological traits, such as body size (De Bie et al., 2012), generation time (Meutter et al., 2007), feeding habits (Cai et al., 2017), rarity (Siqueira et al., 2012) and habitat specialization (Pandit et al., 2009), have also been considered in recent studies. However, previous studies only used spatial eigenvectors (e.g., PCNMs, MEMs or AEMs) as proxies for overall dispersal-related processes, but have rarely considered mass effects and dispersal limitation as largely independent ecological processes shaping biological communities deconstructed by traits (Chaparro et al., 2018; Li et al., 2020).

River networks in mountainous regions provide ideal arenas to simultaneously examine the joint effects of multiple ecological factors on metacommunity organization, as they incorporate high environmental heterogeneity, complex topographic features and variable spatial configurations (Tockner et al., 2010; Li et al., 2020). Mountain rivers also harbor a high freshwater biodiversity, especially of benthic macroinvertebrates, an important organismal group that has been widely used in both fundamental and applied ecological research in aquatic ecosystems (Jacobsen et al., 1997; Clarke et al., 2008; Chang et al., 2014). Macroinvertebrates show a great potential for trait-based studies, since they comprise a very diverse group possessing various life history strategies. For example, macroinvertebrates can be assigned into aquatic, aerial passive and aerial active dispersal groups based on their dispersal mode (Csercsa et al., 2019), or into groups based on their maximal body size (Poff et al., 2006). Macroinvertebrates can also be divided into different environmental tolerance groups, which have been widely used as ecological indicators in bioassessment programs (Chang et al., 2014).

Here, we focused on a nested study design involving 90 river sections distributed among seven subtropical rivers that are largely isolated from each other by mountains. We analyzed data on the overall macroinvertebrate metacommunity and several sub-metacommunities characterized by deconstructing the overall metacommunity based on traits (i.e., dispersal mode, body size and environmental tolerance). Then, we examined the pure and joint effects of environmental filtering, within-river spatial structuring (potentially indicative of mass effects) and among-basin constrains (mainly referring to dispersal limitation) on these community structure using constrained ordination analysis and associated variance partitioning. Under the prevailing perspectives of metacommunity ecology, we hypothesized that (H_1) environmental filtering, mass effects and dispersal limitation all play important role in structuring macroinvertebrate communities; (H_2) the relative importance of the three groups of ecological factors vary depending on the traits used for deconstructed sub-metacommunities. Specifically,

a. for dispersal mode groups, we predicted that the importance of environmental filtering should decrease from i) aerial active dispersers and ii) aerial passive dispersers to iii) aquatic dispersers (Heino 2013). This is because macroinvertebrates with winged adults are always better overland dispersers that can track environmental gradients more closely and find suitable habitats more effectively than those strictly relying on aquatic dispersal (Kärnä et al., 2015; Li et al., 2016).
b. for body size groups, we predicted that the smaller the body size of macroinvertebrates, the greater the effects of environmental filtering. This assumption was based on previous empirical evidence that dispersal ability (here, the capacity of passive long-distance dispersal aided by water, wind or animals) generally increases with decreasing body size (Shurin et al., 2009). We also expected that species with larger body size should show stronger signals of dispersal limitation (De Bie et al., 2012). It should be noted that body size is only a coarse proxy of dispersal ability. However, it may be an alternative when we classify taxa into dispersal ability groups but do not have adequate species- or genus-level information.
c. for environmental tolerance groups, we expected that intolerant taxa may be more strongly associated with environmental filtering than moderately tolerant and tolerant taxa. This assumption was based on the idea that intolerant taxa should be more dependent on pristine environments and more sensitive to anthropogenic environmental stressors (Mykra and Heino 2017).

We expected this study will improve our knowledge of mechanisms underlying metacommunity organization in river networks and other freshwater ecosystems. In this vein, increased knowledge should help advancing metacommunity ecology and its applications in bioassessment, which are still inadequately understood (Cid et al., 2020).

2. Methods

2.1. Study area

We have described the study area in our previous publications, but we also provide a brief account here (Li et al., 2019, 2020). This study was conducted in seven tributary rivers (Jin-Shui River, JSR; Yue River,

YR; Jin-Qian River, JQR; Du River, DR; Si River, SR; Qi River, QR; Lao-Guan River, LGR) in the upstream areas of the Hanjiang River (Fig. 1), the largest tributary of the Yangtze River. Located in the Qin-Ba Mountainous Zone, this river basin is known as a transitional area between northern subtropical and warm temperate zones, between Palearctic and Oriental realms, and between Sino-Himalayan and Sino-Japan forest flora. This region possesses plenty of endemic species that are far from being fully explored, which makes it one of the largest subtropical biodiversity hotspots around the world. Being densely covered with mountains (ca. 84% of the study area), the tributary rivers under research are relatively isolated from each other, providing favorable conditions for testing the effects of spatial processes (i.e., high rates of dispersal at the within-river scale and limited dispersal at the among-rivers scale) on biological communities. This region also harbors high macroinvertebrate biodiversity (Li et al., 2019), which also provides a good possibility for examining community assembly mechanisms using deconstructed sub-metacommunities.

2.2. Macroinvertebrate data

We collected macroinvertebrates from 90 stream reaches in seven tributaries of the Han River in April and May of 2017 (Fig. 1). At each reach, we took five replicates using a Surber sampler (500 μm mesh), covering most representative benthic microhabitats present in a riffle section of ca. 100 m. The samples were kept in a portable refrigerator and were taken to the laboratory within five hours. Macroinvertebrate specimens were hand-picked from the sediments, and then were preserved with 10% formalin. Macroinvertebrates were identified to the lowest possible taxonomic level (i.e., species or genus) by using major reference books (Morse et al., 1994; Merritt and Cummins, 1996; Epler, 2001; Holzenthal, 2009; Morse, 2009; Andersen et al., 2013), articles (Brinkhurst et al., 1990; Zhou et al., 2003; Sun and McCafferty, 2008) and online identification resources (https://www.macroinvertebrates.org/). We merged the five replicate samples in each reach to represent the overall macroinvertebrate metacommunity in the study area.

2.3. Environmental variables

A total of 26 environmental variables were measured and used in the analyses (Supplementary file: S1). Channel width, water depth, current velocity, conductivity, turbidity, dissolved Oxygen, pH and water temperature were measured after macroinvertebrate sampling. Then, benthic substrates were classified into five categories (i.e., boulder, cobble, pebble, gravel and sand) based on particle size and their proportions were estimated with the naked eye. At each site, we got water samples below 10 cm of the water surface and took them to the laboratory within the same day to analyze water chemistry parameters. We measured seven chemistry variables including chemical oxygen demand, total phosphorus, potassium orthophosphate, total nitrogen, nitrite, nitrate nitrogen and ammonium in the laboratory based on the relevant standards (see Wei et al., 2002). Finally, using ArcGIS software (version 10.3), we extracted riparian land cover data (2 km long and 0.5 km wide buffer upstream of each site) which was further classified into one of six land-use types: forestland, farmland, grassland, construction, water body and barren land. Then the percentages of these land-use types were counted and used as explanatory factors in the following statistical analyses.

3. Data processing

3.1. Deconstruction of the metacommunity

The overall macroinvertebrate metacommunity was decomposed into nine sub-metacommunities based on species traits (i.e., dispersal mode, body size and environmental tolerance) (Fig. 2). Firstly, we divided the overall metacommunity into three dispersal groups (i.e., aquatic, aerial passive and aerial active dispersers) according to the main dispersal mode in their life stages (Heino, 2013; Csercsa et al., 2019). Aquatic dispersers included taxa that disperse mainly by water flow. Aerial passive dispersers contained taxa with weak wings in the adult stage and that are dispersed passively by wind or animal vectors, while aerial active dispersers comprised taxa with strong wings and that can disperse actively by flying. We obtained genus-level information of

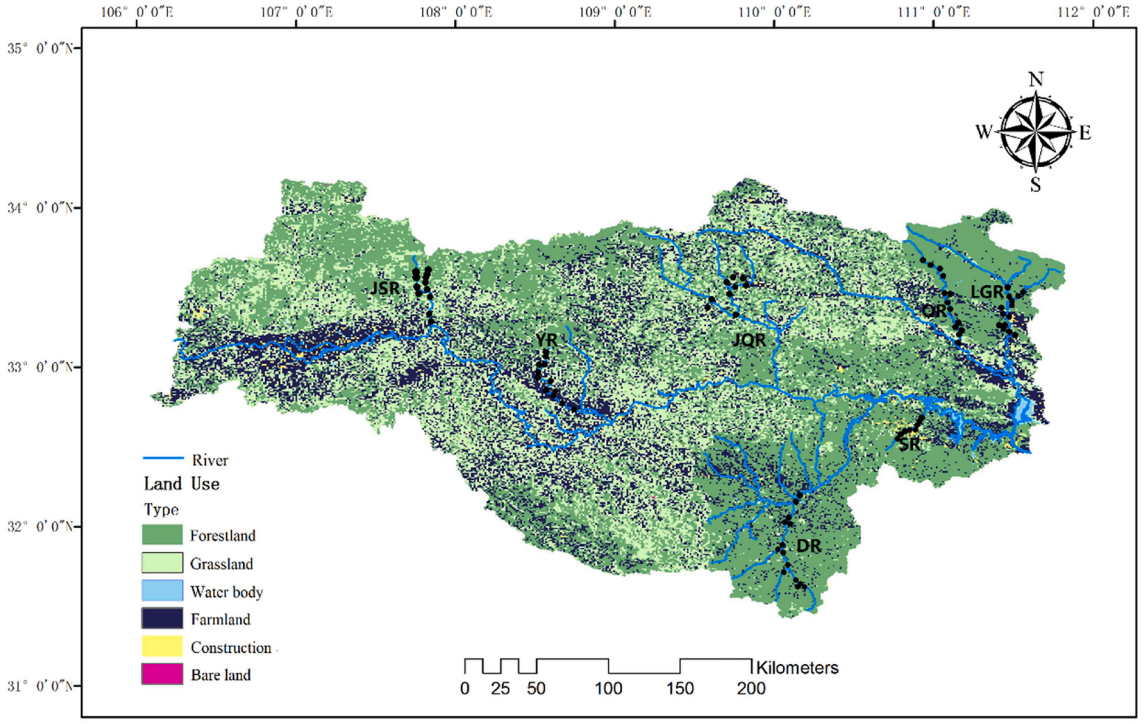

Fig. 1. Map of the study area showing the locations of the 90 sampling sites in the upstream areas of the Hanjiang River Basin.

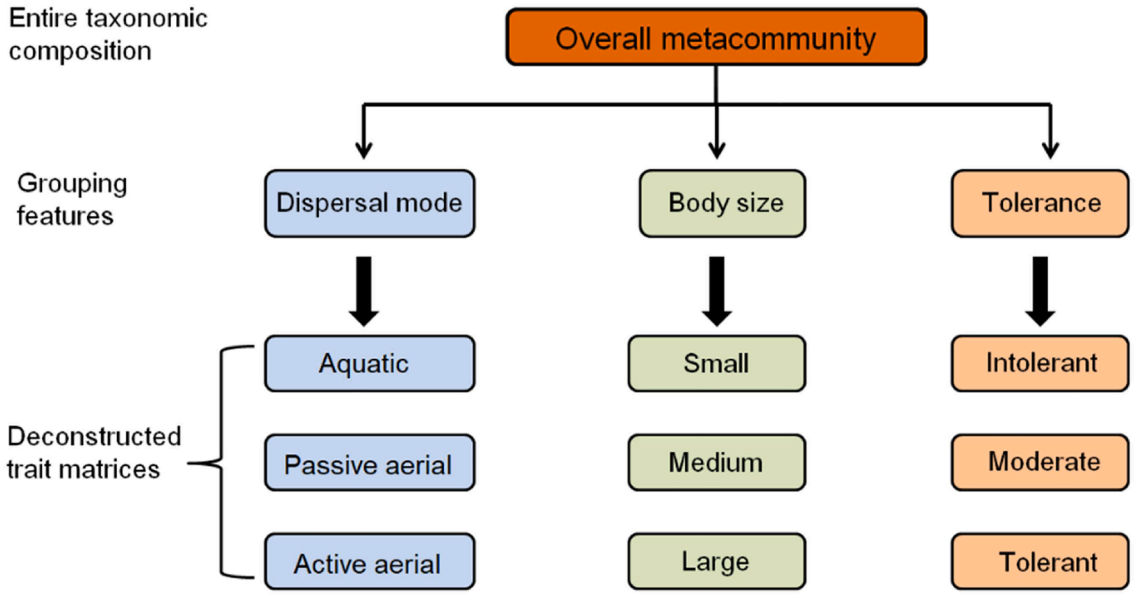

Fig. 2. A schematic figure of the metacommunity deconstruction based on major traits. Macroinvertebrate taxa were first assigned into different traits according to their dispersal mode, body size and environmental tolerance, and then the overall metacommunity matrix was deconstructed into several sub-metacommunity matrices (Table S3).

dispersal mode by referring to Li et al. (2016). Secondly, we obtained three sub-metacommunities based on body size groupings. The overall metacommunity was thus decomposed into groups with small (<9 mm), medium (9–16 mm) and large (>16 mm) body size (Poff et al., 2006). Thirdly, based on their tolerance value (TV), we assigned macroinvertebrates into three groups: intolerant (TV $\leq$ 3), moderately tolerant (3–7) and tolerant (TV $\geq$ 7) (Wang and Yang, 2004). Tolerance value (ranging from 0 to 10) was first used to describe the resistance of taxa to water pollution (Lenat, 1993). It reflects the tolerance of a species to external factors (both physical and chemical), and can also be used to depict environmental adaptability of organisms (Wang and Yang, 2004). All the trait information was double checked by referring to the relevant Chinese books, articles and network resources. We thus obtained a total of 10 metacommunity dataset (site-taxon abundance), including the overall metacommunity and 9 deconstructed sub-metacommunities (Fig. 2).

3.2. A proxy for mass effects

Dispersal is an extremely complicated ecological mechanism that is difficult to quantify in a multi-species metacommunity context. Thereby, ecologists are forced to employ proxies (e.g., spatial eigenfunction analysis) to quantify dispersal process indirectly (Heino et al., 2017a).

Here, we used the method proposed by Declerck et al. (2011) to create spatial factors representing spatial processes within each tributary river. This spatial analysis has been proven to be appropriate for sampling designs across several regions that are separated from each other (Viana et al., 2016; Rocha et al., 2017; Li et al., 2020). We used the function "create.MEM.model" in the R software to conduct this analysis (Declerck et al., 2011). As the sampling sites within each tributary river are relatively close to each other, one can assume frequent dispersal of individuals among these sites, and we thus assumed that the within-river spatial signals, if detected, should be potentially indicative of mass effects. We obtained a total of 24 spatial factors (Moran's eigenvector maps, MEMs) by running this analysis.

3.3. A proxy for dispersal limitation

Following the idea of several previous relevant studies (Declerck et al., 2011; Heino et al., 2017b; Rocha et al., 2017), we created a dummy variable "basin identity" to represent spatial effects in the among-rivers scale. Significant effects of "basin identity" can be considered as a signal of dispersal limitation within an ecological time frame or caused by historical and evolutionary factors (e.g., the influence of biogeography or species pool) or both, with the ecological interpretation depending on the spatial extent under research (Heino et al., 2017b, Gonzalez-Trujillo et al., 2020).

3.4. Ecological factors shaping community structure

The main phases of the data analyses in this study can be seen in Fig. 3. To determine the key ecological factors (i.e., environmental factors, spatial factors and basin identity) for variation in macroinvertebrate communities, we used Redundancy Analysis (RDA) (Legendre and Legendre, 2012). Before the analysis, community abundance data were Hellinger-transformed, while non-normally distributed environmental variables were subjected to log (x + 1) transformation. Of the highly correlated (Pearson's r > 0.75) environmental variables, only one was kept and used in further statistical analyses. Thereafter, a forward selection procedure was employed to select the most influential factors that significantly accounted for variation in community structure ($p <$ 0.05, based on 999 random permutations) from each variable group separately. Forward selection was conducted using the function "ordiR2step" in the vegan package. To reveal the relative importance of the three variable groups, we carried out a variance partitioning analysis (Legendre and Legendre, 2012). The total explained variation in community structure was thus decomposed into pure and shared fractions that were accounted for by the three variable groups. Variance partitioning was conducted using the function "varpart" in the vegan package. We reported adjust R^2 value of each fraction, owing to its impartiality (Peres-Neto et al., 2006). We ran all of the analyses based on the overall metacommunity and the 9 deconstructed communities respectively. RDA and variance partitioning were performed in R software version 3.0.2.

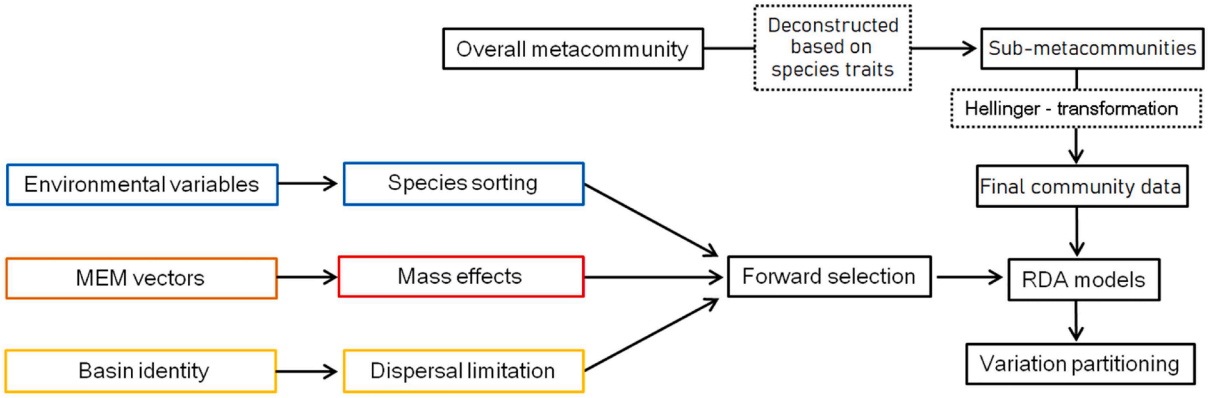

Fig. 3. A schematic diagram showing the analytical methodology used in this study.

4. Results

4.1. Environmental features and community composition

All of the 26 measured environmental factors exhibited considerable variability across the 90 stream reaches from the seven rivers (Supplementary file: Table S1 and S2), implying strong environmental gradients in the study area.

Overall, 275 taxa were identified, belonging to 92 families, 21 orders, 9 classes and 5 phyla. Of these taxa, 86, 92 and 97 were classified into aquatic, aerial passive and aerial active dispersal groups, respectively; 141, 77 and 57 were assigned into taxa groups with small, medium and large body size; 75, 130 and 70 were determined as intolerant, moderately tolerant and tolerant species (Table S3).

4.2. Key environmental variables

In general, conductivity (EC, 8 times), channel width (Width, 8 times), %boulder (7 times) and %Farmland (6 times) were the most commonly selected environmental variables in the models. Other important factors, including %grassland, %cobble, total nitrogen (TN), and %pebble, were also selected at least four times (Fig. 4).

4.3. Relative importance of potential underlying ecological processes

As shown by the results of variance partitioning, environmental factors, within-river spatial factors (potentially indicating mass effects) and basin identity (mainly representing dispersal limitation) all played important roles in structuring macroinvertebrate communities based on both unique and joint fractions (Figs. 5 and 6). Twenty-four percent of the variation in the overall metacommunity was accounted for by the three variable groups. With regard to the unique fractions, pure effect of environmental factors (4%) was slightly more influential than those of mass effects (3%) and dispersal limitation (2%) (Fig. 5).

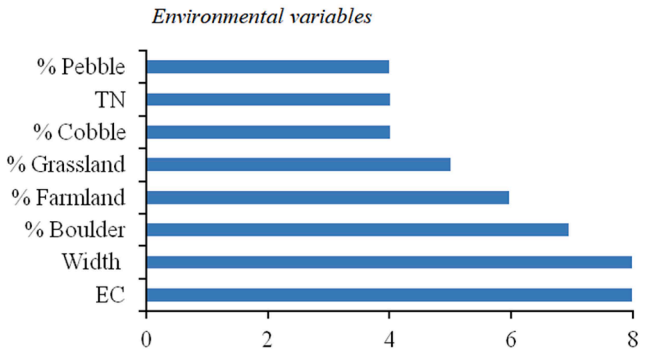

Fig. 4. Frequencies of the environmental variables selected in the forward selection procedures. Abbreviations of the factors can be found in the supplementary file Table S1.

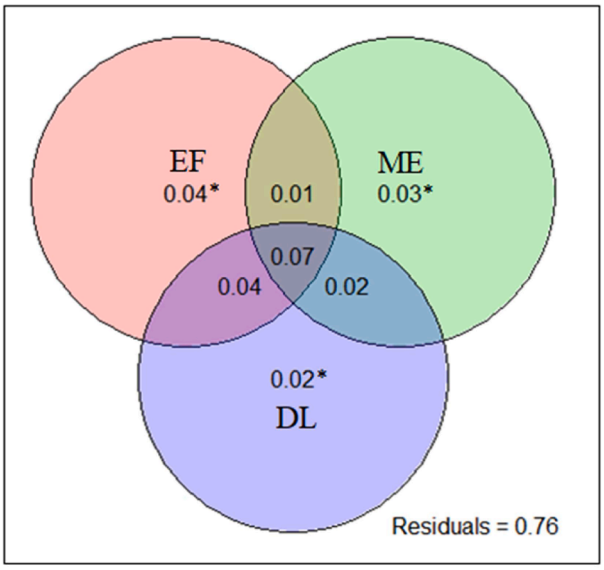

Fig. 5. Venn diagram illustrating results of variation partitioning for the overall macroinvertebrate metacommunity. Values in the circles indicate the amount of variation in the community composition data explained by environmental factors (EF), mass effects (ME) and dispersal limitation (DL), and shared component. Residuals are shown in the lower right corner. All fractions ($^*p < 0.05$) are based on adjusted R^2 values shown as percentages of total variation.

For the dispersal mode groups, the total explained variation ranged from 16% to 30%. Pure fraction explained by environmental factors was highest for aquatic dispersers (6%), followed by aerial active (5%) and aerial passive dispersers (3%). In contrast, pure fraction of mass effects was highest for aerial active dispersers (5%), but much lower for aerial passive (2%) and aquatic dispersers (0) (Fig. 6a). Dispersal limitation generally explained an equal proportion of variation in the community structure of the three dispersal mode groups.

As for taxa with different body size, environmental factors were more influential for large-sized taxa (8%) than for small-sized (4%) and medium-sized (2%) taxa. Mass effects explained a considerable amount of variation in medium-sized taxa group (6%), but appeared almost negligible for small- and large-sized groups. Dispersal limitation was slightly more influential for the large- (2%) than for the small- and medium-sized taxa (Fig. 6b).

Regarding macroinvertebrate groups with different environmental

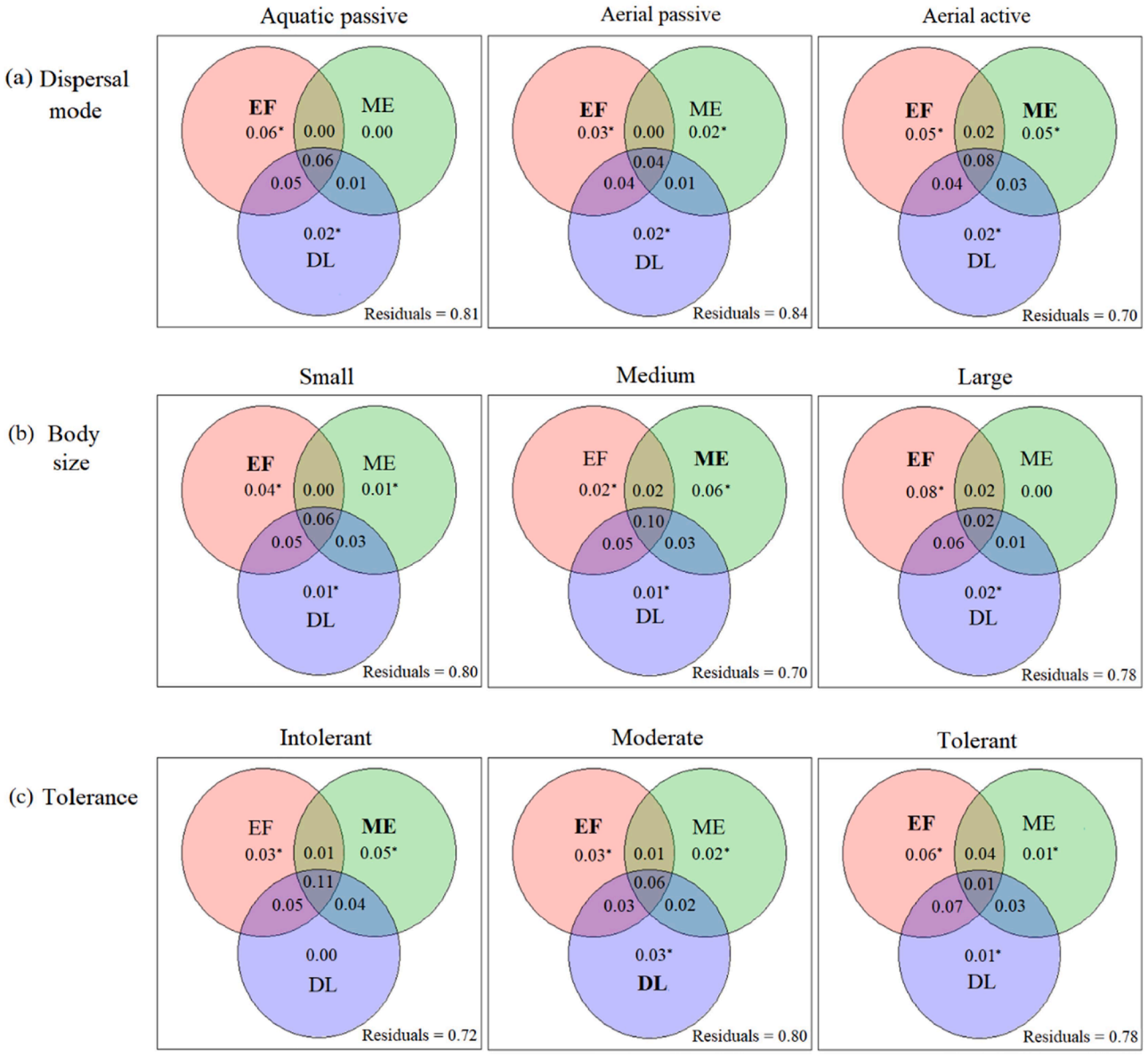

Fig. 6. Venn diagrams illustrating results of variation partitioning for different deconstructed trait groups: (a) Dispersal mode, (b) Body size and (c) Environmental tolerance. Values in the circles indicate the amount of variation in the community composition data explained by environmental factors (EF), mass effects (ME) and dispersal limitation (DL), and shared component. Residuals are shown in the lower right corner. All fractions ($*p < 0.05$) are based on adjusted R^2 values shown as percentages of total variation in community structure. The greatest effects for community structure were highlighted in bold.

tolerances, environmental factors alone explained more of the variation in tolerant taxa (6%) than in intolerant (3%) and moderately tolerant taxa (3%) groups, while mass effects accounted for more variation in intolerant taxa (5%) than in moderately tolerant (2%) and tolerant taxa (1%). Pure fraction of variation explained by dispersal limitation for moderately tolerant taxa was higher than for tolerant and intolerant taxa (Fig. 6c).

Remarkably, the shared fractions for both overall metacommunity and the deconstructed sub-metacommunities were also considerable in the models, indicating the existence of shared spatial and environmental effects on metacommunity organization.

5. Discussion

Ecologists have been increasingly focusing on the relative contributions of spatial and environmental factors to variation in community structure in the last three decades (Borcard et al., 1992; Borcard and Legendre, 2002). Even though this approach is appealing, it has also spurred criticism owing to problems with the ecological interpretations based on statistical patterns (Gilbert and Bennett, 2010; Smith and Lundholm, 2010). They may sometimes fall short in providing a more comprehensive picture of how a metacommunity is assembled owing to problems in defining and interpreting the spatial effects in multivariate analysis (Heino et al., 2017a). In this study, we applied a modified approach based on spatial eigenfunction analysis (Declerck et al., 2011) by decomposing spatial effects into processes acting at within-river (mainly pertaining to mass effects; e.g., Heino et al., 2013) and among-rivers (mainly caused by dispersal limitation; e.g. Li et al., 2020) scales. This approach comprising nested spatial scales allowed us to test the relative importance of environmental filtering, mass effects and dispersal limitation simultaneously for macroinvertebrate communities in a river network typical of mountainous landscape.

Generally, our results revealed that the three main ecological processes all played important roles in community assembly, thereby

supporting our first hypothesis (H_1). According to previous studies, environmental filtering is the dominant process shaping metacommunity organization within a drainage basin, while spatial processes often appear to be less significant (Siqueira et al., 2012; Rádková et al., 2014; Jamoneau et al., 2017; De Campos et al., 2018). Through decomposition of spatial effects into those resulting from high (e.g., mass effects) and low (e.g., dispersal limitation) potential dispersal rates, we obtained results slightly differing from the findings of previous reports. Although environmental filtering was still the most important process in controlling variation in community structure, the influences of mass effects and dispersal limitation could not be neglected. It is worth noting that the sum of the explanatory power of all spatial effects even overrode that of environmental control in half of the cases (Figs. 4 and 5). We thus highlight the relevance of better depicting dispersal-related processes by employing more elaborate approaches based on spatial proxy variables (Padial et al., 2014; Kärnä et al., 2015; Heino et al., 2017a; Sarremejane et al., 2017).

Nevertheless, the proportion of explained variation in community structure remained rather low (16–30%), as has also been found in previous studies on the community assembly of freshwater macroinvertebrates using constrained ordination approaches (Cai et al., 2017; Lansac-Toha et al., 2019; Gonzalez-Trujillo et al., 2020). Some potentially important factors regulating variation in the present metacommunity structure may be neglected, such as environmental variables that were not measured, inadequate modeling of spatial processes and stochastic events, which may account for this unpredictability in metacommunity structure (Heino et al., 2015; Rocha et al., 2017). Although we are confident that we have considered the most important predictor variables in our study, we cannot rule out the possible consequences of stochastic events on community structure (Hubbell, 2001; Lansac-Toha et al., 2019). Some of these stochastic events (e.g., flood disturbances, abrupt changes in environmental conditions, and random local extinctions), however, cannot be easily quantified and coded into factors suitable for statistical analysis and, thus, could not be considered in this study. The low explanatory powers of the models may also be attributed to the fact that we did not consider the possible importance of interaction between traits (e.g., body size × tolerance). Therefore, combining different traits into unique trait combinations might result in higher levels of explained variation than what one obtains by using whole metacommunity or individual traits (Tolonen et al., 2016).

The relative influence of environmental filtering, mass effects and dispersal limitation largely depended on the traits of organisms (supporting H_2), as was detected in our results and other relevant studies (Cañedo-Argüelles et al., 2015; Tolonen et al., 2016; Lindholm et al., 2018). Therefore, it is obvious that the deconstructive approach based on traits can facilitate our understanding of the mechanisms underlying community assembly across broad spatial extents. However, only some of our *a priori* expectations were supported. For dispersal mode, we expected that the relative importance of environmental filtering should decrease in the following order: aerial active dispersers > aerial passive dispersers > aquatic dispersers (Heino, 2013). We found that our results differed from what was expected, as aquatic dispersers were most strongly affected by environmental factors. This result may be due to the fact that aquatic dispersers are better at tracking environmental gradients in this particular river basin. However, the two aerial dispersal groups showed stronger relative effects of spatial factors on community structure. Aerial dispersers (especially aerial active dispersers) possess stronger dispersal ability, and thus are more likely to be influenced by mass effects at the within-river scale (Heino et al., 2015; Tornero et al., 2018). Mass effects can decouple the expected associations between biological communities and environmental factors (Heino et al., 2017a), and may even override the influences of environmental filtering in some highly-connected systems (Cai et al., 2017; Tolonen et al., 2017; Corte et al., 2018; Ptatscheck et al., 2020). This may be a reason why the sub-metacommunities comprising aerial dispersers showed stronger spatial structuring in comparison with aquatic dispersers.

With regard to body size groups, we predicted that the sub-metacommunities comprising smaller-sized taxa are strongly linked to environmental filtering, while large-sized taxa may be more strongly controlled by dispersal limitation (i.e., among-basin constraints). This assumption was partially supported, as dispersal limitation indeed accounted for more of the variation in the sub-metacommunities comprising the large-sized taxa. Surprisingly, small- and medium-sized taxa groups showed environmental control that was much weaker than that for the large-sized group. There are a number of reasons that may explain this counterintuitive finding. Firstly, strong links between small- and medium-sized taxa and environmental factors may be decoupled by mass effects as a result of high dispersal rates (Heino et al., 2015). Secondly, macroinvertebrates with large body size can direct their dispersal and thus are more likely to find habitat patches that are suitable in terms of environmental conditions (Kärnä et al., 2015). On the other hand, small-sized taxa may be more likely to suffer from stochastic events (e.g., random local extinctions) (Ptatscheck et al., 2020). For instance, small organisms typically have relatively short generation times and high population growth rates, but also face the high mortality risks caused by predation and disturbance (Logerwell and Ohman, 1999; Preisser and Orrock, 2012). Some studies suggested that body size alone may be not a good proxy for dispersal ability (e.g., Heino et al., 2017a), since body size is also strongly related to other fundamental biological processes, such as metabolism, reproduction rate and the likelihood of extinction (Allen et al., 2006; Preisser and Orrock, 2012).

For the environmental tolerance groups, we expected that environmental filtering should be more influential for intolerant taxa than for moderate and tolerant taxa. However, counterintuitively, environmental filtering generally explained more of the variation in the community structure of the tolerant group, and intolerant and moderately tolerant groups were highly structured by dispersal-related processes (mass effects and/or dispersal limitation). This finding may be linked to factors other than environmental tolerance, such as that different proportions of specialists and generalists (Rádková et al., 2014), common and rare species (Siqueira et al., 2012), or weak and strong dispersers (Sarremejane et al., 2017) occur among taxa in different environmental tolerance groups. Since this finding may appear counterintuitive, more detailed autecological studies are also needed to classify taxa into tolerant and intolerant groups. Although not supporting our expectation, this finding may provide some implications for biomonitoring in a metacommunity context (Cid et al., 2020). For example, biomonitoring programs may be less effective in discerning impaired sites in this basin when using intolerant taxa as ecological indicators, since the migration of individuals of these taxa from pristine sites to nearby impacted sites may be high (Heino et al., 2017a).

6. Conclusions

Our study contributed to metacommunity research in riverine ecosystems by integrating multiple ecological processes underlying variation in community structure. The present results showed that environmental filtering, mass effects and dispersal limitation play potentially important roles in the community assembly of riverine macroinvertebrates, but their relative importance largely depended on biological traits. Therefore, two major points of our study should be highlighted. Firstly, the decomposition of spatial processes into potential proxies of dispersal limitation and proxies of mass effects resulted in improved estimates of the importance of spatial processes compared with many previous studies. Secondly, the deconstructive approach based on biological traits can enhance our knowledge of community assembly by providing a more predictive framework of metacommunity ecology and applied river research. Our results also provide implications for bioassessment. For instance, bioassessment programs may be highly biased if we use such organismal groups as ecological indicators that show strong association with dispersal-related processes.

CRediT authorship contribution statement

Zhengfei Li: Conceptualization, Methodology, Writing - original draft. **Jani Heino:** Writing - original draft. **Xiao Chen:** Visualization, Investigation. **Zhenyuan Liu:** Macroinvertebrate sampling, Environmental factors measuring. **Xingliang Meng:** Macroinvertebrate sampling, Environmental factors measuring. **Xiaoming Jiang:** Macroinvertebrate sampling, Environmental factors measuring. **Yihao Ge:** Macroinvertebrate sampling, Environmental factors measuring. **Juanjuan Chen:** Writing - original draft. **Zhicai Xie:** Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107188.

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